

# THE SWIMMING PLANE OF THE CRUSTACEAN *MYSIDIUM GRACILE* (DANA)<sup>1</sup>

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An animal creeping on the ground or on any other solid surface can turn freely only around its dorso-ventral axis. Direct contact with the substrate largely maintains and stabilizes its equilibrium. This is not so, in contrast, for an animal swimming freely in water where such mechanical constraint for turning is absent. Hence the organism's rather labile orientation in space must be controlled continuously so that turbulence of the medium and the inevitable asymmetries in locomotor activity will not cause an erratic course.

In a free-swimming mysid, roll and pitch are under the joint control of orientation transverse to gravity and the dorsal light reflex (Delage, 1887; Bethe, 1895; Bauer, 1908; von Buddenbrock, 1914; Foxon, 1940). Yaw or lateral turning deviations can be checked with the help of polarized light (Bainbridge and Waterman, 1957, 1958; Jander and Waterman, 1960; Waterman, 1960), and when the mysids are positively or negatively phototactic with the direction of a light source (Franz, 1911, 1913; Fraenkel, 1931).

Food finding demands a succession of turning movements inconsistent with a completely rigid control of body position. In mysids, as in bottom-living animals, such searching movements consist almost exclusively of turns about the dorso-ventral axis. Usually rotations about the longitudinal axis and the transverse axis appear only as minor deviations (Cannon and Manton, 1927), although turning about the transverse axis is evoked by hydrostatic pressure changes which result in upward or downward swimming (Rice, 1961). This close control of pitch and roll, coupled with at least temporary extensive spontaneous turnings to the right and to the left, maintains the individual mysid's position within an imaginary plane, which will be referred to as the swimming plane (Fig. 1).

Since the mysid's equilibrium, and hence the inclination and stability of the swimming plane, are controlled both by light and gravity, the question arises how such oriented behavior is altered with changes of intensity and direction of illumination. Of particular interest are those cases in which the two modes of orientation are opposed to each other because behavior in the conflict situation may make possible some inferences concerning the mechanism involved. The present studies are comparable in approach to previous much more detailed investigations on fish orientation (von Holst, 1935, 1950; Braemer, 1957, 1958).

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### METHODS

All experiments were performed at the Bermuda Biological Station on *Mysidium gracile* (Dana) collected from a marine pond. A small all-glass aquarium ( $4 \times 8 \times 9$  cm.), containing some 20 recently caught animals, was illuminated from a distance of 20 cm. by a 6-volt microscope lamp. This produced a circular bright spot with a luminance of 170 candelas/cm.<sup>2</sup> and subtending a visual angle of  $8^\circ$ . No effort was made to measure the small amount of diffuse light present in the experimental dark room.

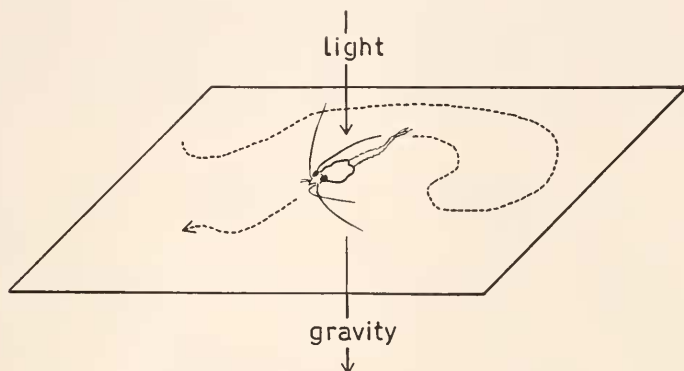


FIGURE 1. The normal swimming pattern of *Mysidium gracile*, showing the swimming plane perpendicular to the direction of light and gravity. Turning occurs almost entirely within this plane.

A series of exposures was taken with a still camera to determine the mysid's angular orientation under each of the different experimental conditions. When the animals were in total darkness, photographs were taken with an electronic flash. The positions of the body axes were measured on the projected negative of the film, summed over 5-degree intervals, and then plotted on polar coordinates as shown in Figures 2-6. During the experiments conditions were changed from exposure to exposure to minimize the effect of any drift in time.

- Abbreviations:  $m$  = Mean angular measurement.  
 $s$  = Standard deviation of the mean.  
 $n$  = Number of individual readings.  
 $0^\circ$  = Upward direction relative to gravity.

### RESULTS

Three experiments were done, one with vertical illumination and two with horizontal.

TABLE I  
Data of Experiment 1

Condition	Axes					
	Longitudinal			Transverse		
	<i>m</i>	<i>s</i>	<i>n</i>	<i>m</i>	<i>s</i>	<i>n</i>
<i>a</i> (dark)	91° ± 1.8°	±24.3°	218	88.8° ± 2.2°	±9.2°	17
<i>b</i> (light)	90.1° ± 1.6°	±27.1°	215	89.2° ± 1.8°	±9.3°	26

*Experiment 1.* Samples of the mysids' angular orientation were recorded under two conditions: (*a*) in total darkness and (*b*) with a vertical light beam from above. In *a*, only gravity orientation could be effective, whereas in *b*, light could give additional directional clues. The data thus obtained show that under both Conditions *a* and *b* the swimming plane was horizontal. With or without the light from above, the longitudinal and the transverse axes were maintained

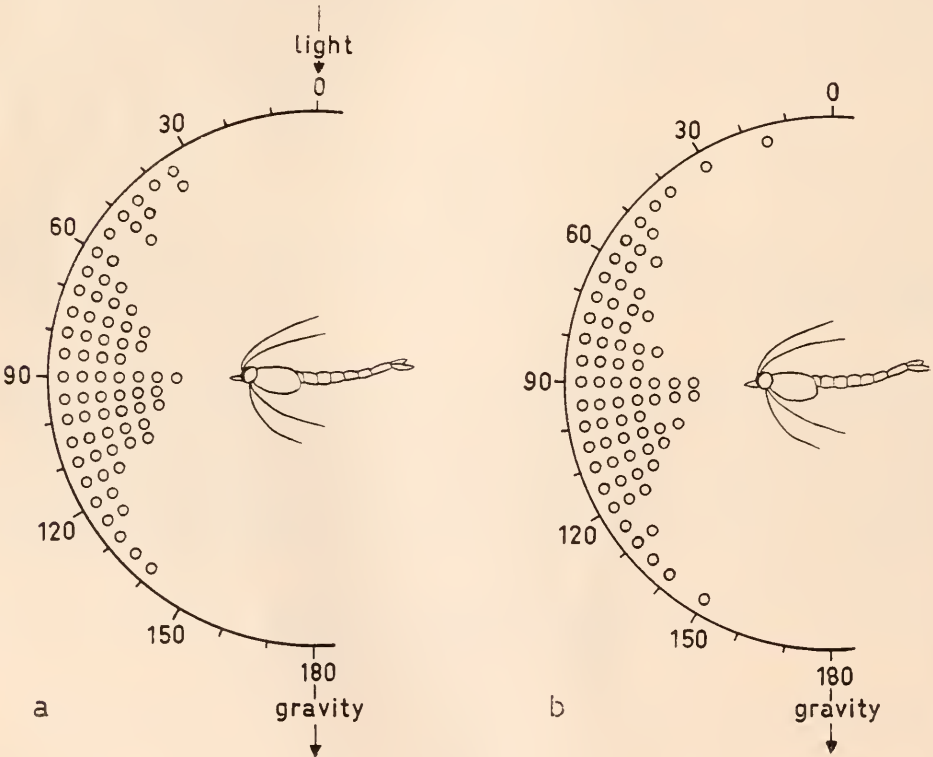


FIGURE 2. Positions observed for the longitudinal axis of swimming *Mysidium* when stimulated by light and gravity (*a*), and when stimulated by gravity alone (*b*). Each small circle represents three readings. Experiment 1.

in the same horizontal positions and, remarkably enough, addition of light as a second source of directional information had no effect on the random fluctuations in the positions of the two axes (Table 1 and Figs. 2 and 3).

If the accuracy of orientation about the two axes is compared by averaging the data for Conditions *a* and *b*, the fluctuations for the longitudinal axis ( $s = \pm 25.1^\circ$ ) are seen to be 2.7 times larger ( $p < 0.1\%$ ) than those for the transverse axis ( $s = \pm 9.2^\circ$ ). This difference is due to apparently spontaneous

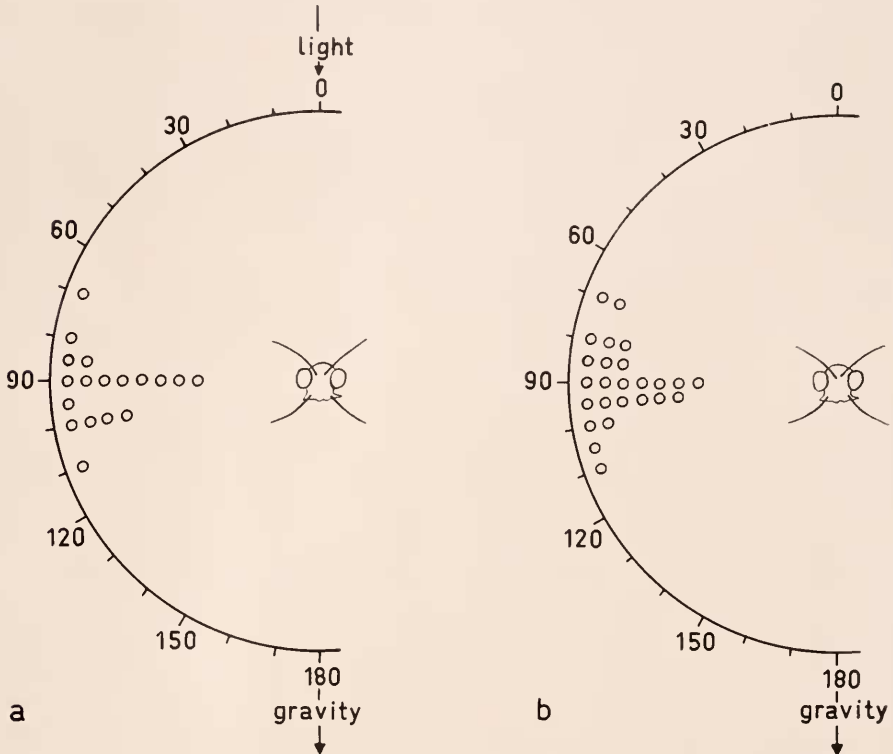


FIGURE 3. Positions observed for the transverse axis of swimming *Mysidium* when stimulated by light and gravity (*a*), and when stimulated by gravity alone (*b*). Each small circle represents one reading. Experiment 1.

up and down undulations of the mysid's swimming path which may be connected with food finding, since such oscillations increase conspicuously after edible particles have been added to the water. Somewhat comparable undulations in the swimming path of *Palaeomon northropi* have been observed in the field (Bainbridge and Waterman, 1957).

This experiment with vertical illumination seems to show that directional light has no effect whatever on the orientation of *Mysidium*. That this is not so can be shown by changing the direction of the incident light as in the following experiment.

*Experiment 2.* This time the light beam entered the vessel horizontally. The

camera was photographing horizontally at  $90^\circ$  to the beam of light. Again records were taken under two conditions. In Condition *a* the light source had its full intensity and in Condition *b* this was reduced by a neutral filter to 6.3% of the original value.

The results are shown in Table II and Figures 4a, b and 5a, b. Under Condition *a*, the longitudinal axis was tipped from its original horizontal position (Experiment 1) approximately  $63^\circ$  upward or downward so that the mysid's dorsal surface was turned partly toward the light source. With the lower light intensity the longitudinal body axis was tilted in the same way but only through about  $51^\circ$  instead of  $63^\circ$ . This reduction of the inclination with reduced light intensity is significant ( $p < 1\%$ ).

The horizontal illumination caused the transverse axis also to be turned away from its horizontal position though to a lesser degree than the longitudinal axis (Fig. 5a, b). Again the direction of tilt was such that the dorsal surface turned partly toward the light source. The degree of this turning was intensity-

TABLE II  
*Data of Experiment 2*

Condition	Axes					
	Longitudinal			Transverse		
	<i>m</i>	<i>s</i>	<i>n</i>	<i>m</i>	<i>s</i>	<i>n</i>
<i>a</i> (bright)	$26.1^\circ \pm 1.4^\circ$ $152.7^\circ \pm 3.0^\circ$	$\pm 20.6^\circ$	231 39	$35.0^\circ \pm 1.6^\circ$	$\pm 12.4^\circ$	57
<i>b</i> (dim)	$38.2^\circ \pm 1.8^\circ$ $136.6^\circ \pm 3.3^\circ$	$\pm 20.6^\circ$	126 49	$45.0^\circ \pm 2.1^\circ$	$\pm 14.2^\circ$	47

dependent ( $55.0^\circ$  for Condition *a* and  $45.0^\circ$  for Condition *b*) as in the case of the longitudinal axis. Note that again *s* for the longitudinal axis was appreciably greater ( $\pm 20.6^\circ$ ) than for the transverse axis ( $\pm 13.3^\circ$ ). Turning the light source through  $90^\circ$  from Experiment 1 to Experiment 2 gave rise to turning of the two body axes in the same direction (*i.e.*, dorsum towards the light) but through less than  $90^\circ$ .

These facts can only mean that (1) the light beam is indeed being used as a means of orientation, and (2) an additional mode of orientation is present which can use only gravity for a reference direction. This demonstrates again what has been known already (references cited in the introduction), namely that in mysids phototactic and geotactic orientation take place simultaneously. Experiment 1 shows that there is no conflict between geotaxis and phototaxis with a light source in the zenith. From Experiment 2, however, opposed effects of geotaxis and phototaxis can be inferred; this is resolved by the mysids with a compromise reaction. Even in this conflict situation a swimming plane is maintained. Although slanted this plane is still flat and not warped as one might expect in view of the different inclinations of the two body axes involved. This flatness is maintained because progression usually is head first and not oblique or sideways.

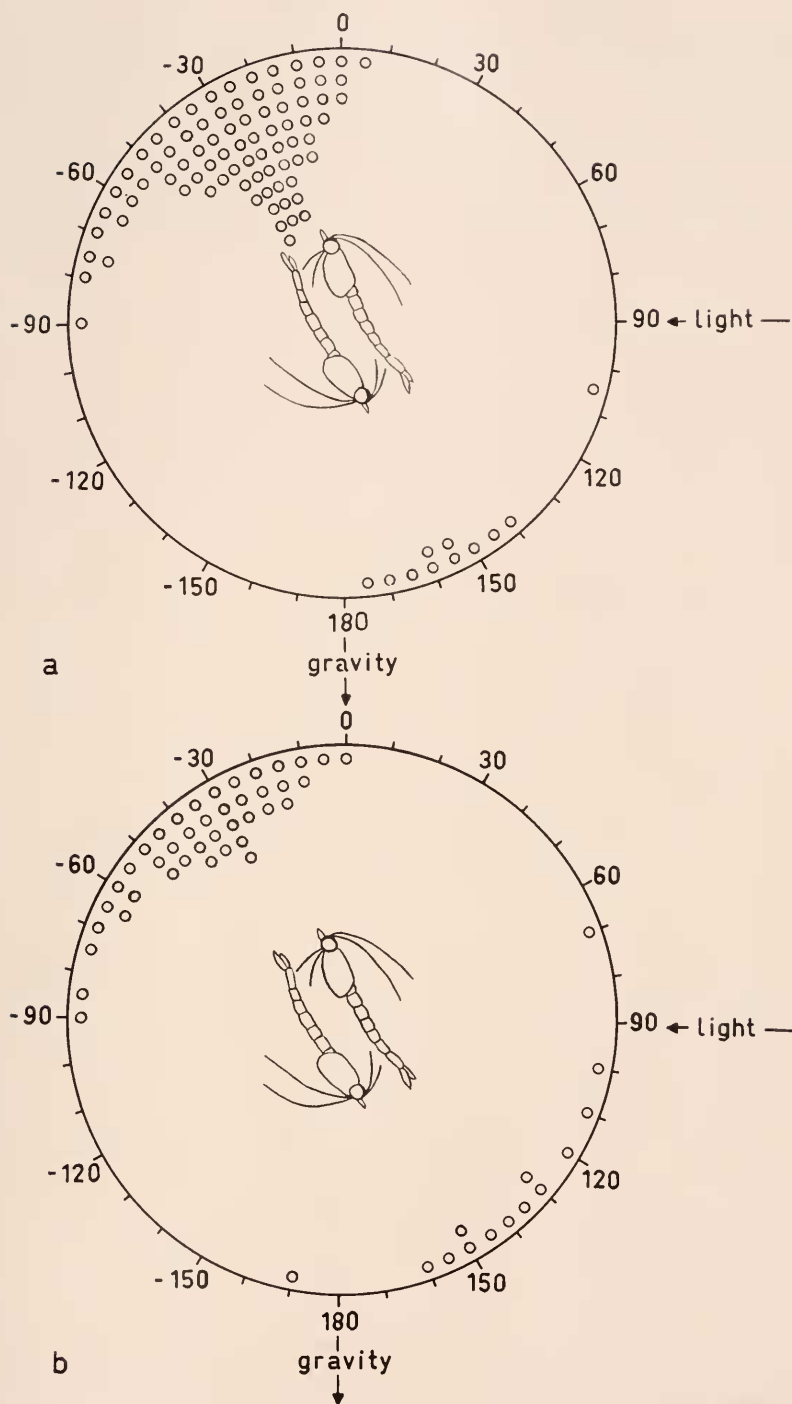


FIGURE 4. Positions observed for the longitudinal axis of swimming *Mysidium* when the light beam stimulates with full intensity (a), or with reduced (6.3%) intensity (b), horizontally in the plane of the paper. Each small circle represents three readings. Experiment 2.



*Experiment 3.* Since the dorso-ventral axis in Experiment 2 was always slanted in the field of gravity, geotactic orientation about this axis was possible for geometrical reasons. To determine whether orientation of this sort does in fact take place, the stimulus situation was kept the same as in the previous experiment but the camera was aimed horizontally straight towards the beam of light and hence obliquely faced the ventral side of the swimming plane. The data show (Fig. 6) that upward orientation is predominant although all other directions are possible. This asymmetry occurs because the animals spent much time hover-

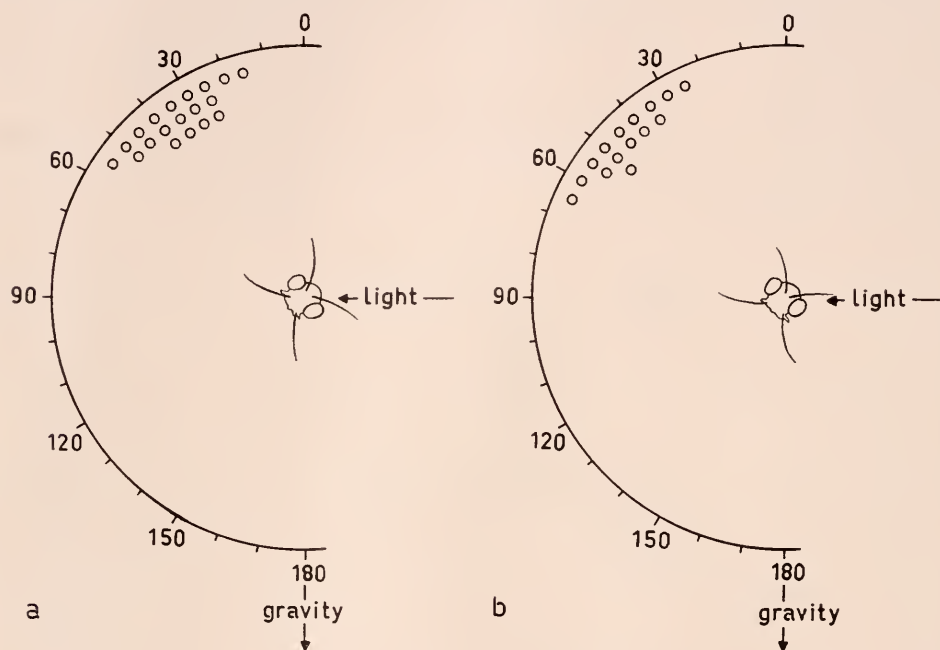


FIGURE 5. Positions observed for the transverse axis of swimming *Mysidium* when the light beam stimulates with full intensity (a), or reduced (6.3%) intensity (b), horizontally in the plane of the paper. Each point represents three readings. Experiment 2.

ing in a head-up position. The continuous distribution of angular positions found in this experiment contrasts markedly with Experiments 1 and 2 (Figs. 2-5) with their limited angular ranges of swimming directions.

The tendency to turn left and right within the slanted swimming plane is therefore greater than the one for turning out of the plane, in spite of the fact that the force of gravity does have a component affecting orientation in such an oblique plane (compare Figs. 4, 5 and 6).

#### DISCUSSION

Interactions of conflicting turning tendencies in response to simultaneous gravitational and optical stimulation have frequently been studied, *e.g.* in molluscs

(Crozier and Wolf, 1929); arthropods (Yagi, 1928; Schöne, 1954, 1959; Jander, 1957, 1960); and vertebrates (von Holst, 1935, 1950; Braemer, 1957, 1958). Usually all these animals, including the present case of the mysids, integrate centrally the conflicting turning tendencies in a way that determines the particular compromise between the two opposing rotations. Thus the actual position assumed indicates the relative strengths of the turning tendencies induced by the different external stimuli. Evidence of these relations can be obtained from the data of Experiment 2.

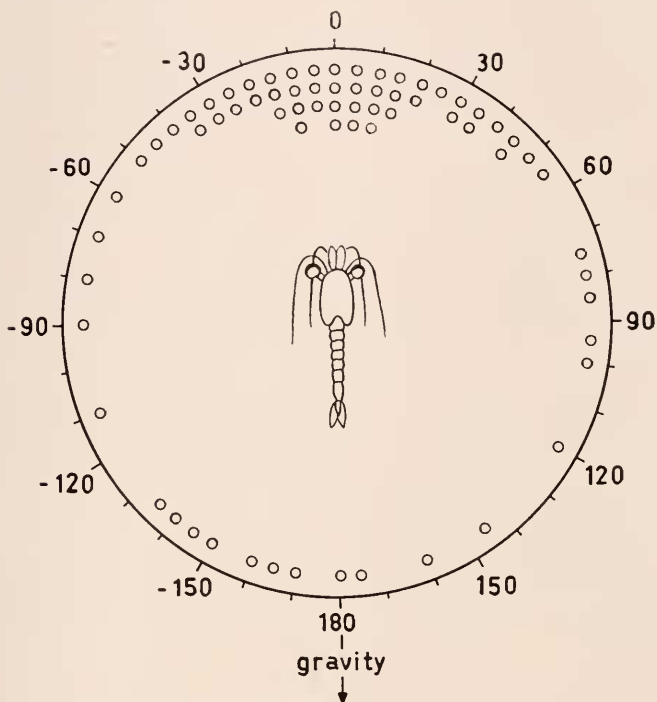


FIGURE 6. Positions observed for the longitudinal axis of swimming *Mysidium* when stimulated by a horizontal light beam (perpendicular to the plane of the paper) and gravity. Each point represents three readings. The inset shows the animal in its most frequent orientation with the longitudinal axis in the plane defined by the directions of light and gravity (the same position is shown from the side in the upper insets in Figure 4). When the longitudinal axis falls outside of this plane, the interaction of light and gravity causes an asymmetry of the eyes in relation to the direction of light as shown in the rare case of a horizontal position of the longitudinal axis illustrated in Figure 5. Experiment 3.

In both Conditions *a* and *b* of Experiment 2, light has more effect on the positions of the longitudinal axis than has gravity. This axis always turned more than  $45^\circ$  in response to shifting the stimulating light beam  $90^\circ$  from the vertical to the horizontal direction (Fig. 4a, b). Using the general rule (Schöne, 1959) that the strength of an animal's dorsal light reflex is proportional to the sine of the angular difference between its actual dorsal direction and the direction of the stimulating light, the relative effectiveness of the two optical stimuli in



Experiment 2 can be estimated. Under Condition *a* (Fig. 4a) the ratio of the gravity-induced turning tendencies to the light-induced ones is equal to the ratio  $\sin 27^\circ : \sin 63^\circ$ , or 1:4.05. A similar calculation for Condition *b* yields a ratio of 1:1.24. Since the gravitational stimulus was constant the 17-fold increase in light intensity must have been responsible for the 3.3-fold (4.05:1.24) increase in the phototactic turning tendency.

A stronger turning tendency with increasing light intensity seems to be the rule for all dorsal light reactions. Such a relationship has been found now in *Mysidium*, in decapods (Schöne, 1954, 1959), in insects (dytiscid larvae, Schöne, 1951), and in fishes (von Holst, 1935; Braemer, 1957, 1958). In contrast, the turning tendencies in positive and negative phototaxes are independent of the stimulus strength in ants (Jander, 1957), bees (Boch, 1957, unpublished), caddis flies (Trichoptera, Jander, 1960) and, on the basis of preliminary studies, in most other holometabolous insects.

Measuring the physiological resolution of conflicting turning tendencies is not the only way of estimating their relative strength. Another method can be derived as follows. The variations or undulations in the position of the body axes measured as standard deviations are the result of two groups of counteracting forces. These are: (1) separate or integrated turning tendencies induced by optical and gravitational stimulation (= tactic forces) which tend to maintain one steady position of the body axes, and (2) the disturbing internal and external randomizing forces, which tend to turn the body axes away from the steady position just mentioned into any position in space. An increase in the strength of the randomizing forces can be expected to augment the standard deviation, and any increase in the strength of the tactic forces can be expected to reduce it.

This second method of estimating the strength of the tactic forces or tendencies with the help of their interaction with randomizing forces has already been successfully applied in caddis flies (Jander, 1960) and *Daphnia* (Waterman and Jander, unpublished). In both cases the results obtained with this method and the other method described above were consistent with each other. However, the mysid results do not yield such a consistent picture.

Experiment 2 demonstrated that both light and gravity together maintain a steady body position. Yet the standard deviations are practically the same in Condition *a* and *b*, and the same holds for Experiment 1. Such stability of the standard deviation must result from a stable balance between the tactic and the randomizing forces. However, Experiment 2 shows that geotactic and phototactic turning tendencies act jointly and that the strength of the latter depends on the light intensity. Hence with the transition from darkness to light in Experiment 1 the combined tactic turning tendencies should be approximately five times larger than the geotactic ones alone (the phototactic turning tendency is four times the strength of the geotactic one according to Experiment 2a). But this expected five-fold increase in tactic tendency would reduce the standard deviation of the axial positions five times. This is definitely not true. Similar considerations hold for Experiment 2.

Such an analysis indicates that the tactic turning tendencies controlling position cannot act merely by algebraic addition in opposing the randomizing forces. Most likely one must assume that they are not only added but also divided by their

combined strength in a way that can be symbolized by

$$\frac{ax + by}{x + y}$$

when  $x$  and  $y$  stand for those parts of the tactic forces which depend on the stimulus strength and  $a$  and  $b$  for those that depend on the stimulus direction. If reciprocal inhibitory processes were at work such an expression might be expected to hold. It should be mentioned in this connection that Schöne (1959, p. 189) was able to show that increasing gravitational stimulation decreases (inhibits) the turning effect of a given light stimulus in crustacean eyestalk movements (*Palaeomonetes*, Decapoda). Note also that maintaining an optimum strength for a turning tendency is advantageous, because too strong a response will result in oscillation due to overshooting, and too weak a response will render the mechanism unnecessarily inefficient.

There are several similarities between the equilibrium orientation of fishes (as analyzed by von Holst, 1935) and of the mysids. Both groups use eyes and statoliths in maintaining a swimming plane and both assume compromise positions in the case of conflict. This compromise orientation depends in fishes and mysids, as well as in other Crustacea (Schöne, 1959, 1961), on the intensity of the stimulating light. In both fishes and mysids the relative orienting efficiency of light compared with gravity is greater around the transverse axis than around the longitudinal axis.

The ecological and adaptive significance of having a swimming plane with the properties described may be seen in the following hypothesis. Swimming in a plane could keep the mysids in a layer rich in planktonic food and may help keep swarms together. In the natural habitat one frequently sees mysids in swarms.<sup>3</sup> Also, in nature *Mysidium gracile* has been repeatedly observed in Walsingham Pond, Bermuda, swimming in slanted planes near underwater cliffs. The reason for the tilted swimming plane in this case was undoubtedly the same as in the laboratory experiments. In this way the mysids can graze within a plane near a cliff with reduced chances of colliding with it.

#### SUMMARY

1. *Mysidium gracile* (Dana) tends to move within a plane, the swimming plane, which is oriented as nearly as possible perpendicular to the directions of light and gravity.

2. Horizontal illumination induces an orientation conflict which is resolved by maintaining the swimming plane in a slanted position intermediate between those positions dictated by the two stimuli.

3. The turning tendencies of the dorsal light reaction increase with increasing light intensities.

4. There is evidence that gravity- and light-induced turning tendencies inhibit each other.

<sup>3</sup> Other factors related to swarming behavior in a second species of *Mysidium* have recently been reported (Steven, 1961).

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